Research Article

Diet comparison suggests limited competition between invasive black rats (*Rattus rattus*) and sympatric endangered rodents

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Abstract

Black rats (*Rattus rattus*) are one of the most widespread invasive animals and have been implicated in the decline of species representing several wildlife taxa, particularly on islands. However, their impact on more closely related species, i.e. rodents, via competition is less well-understood. Using diet similarity as a metric of competition for food resources, we used stable isotopes to compare diets of two populations of black rats to diets of two endangered populations of rice rats (*Oryzomys palustris natator* and *Oryzomys palustris sanibeli*) in southern Florida, USA. Specifically, we analysed hair samples from 32 rice rats and 35 black rats for carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes. In addition, we analysed samples of 129 potential food items to characterise rodent diets using stable isotope mixing models. Despite considerable overlap in isotope-space, we observed differences between rice rats and black rats in the relative composition of plant and animal foods. Specifically, the diets of both populations of rice rats consisted of mostly animal foods, whereas the diets of black rats consisted mostly of plants. In combination with previous work revealing temporal niche partitioning, our results suggest competition between invasive black rats and endangered native rodents may be limited. As such, expensive and logistically complicated efforts to control black rats may have limited success for conserving endangered rodents.

Key words: Florida, island, mangrove, rodent, stable Isotope, Wetland

Introduction

Invasive species represent a growing threat to global biodiversity (Vitousek et al. 1997; Clavero and Garcia-Berthou 2005; Doherty et al. 2016; Spatz et al. 2017). One of the most widespread, prolific and detrimental invasive species on the planet is the black rat (*Rattus rattus*; Drake and Hunt 2009; Spatz et al. 2017). This globally distributed generalist has contributed to declines in native populations, biodiversity and ecosystem function (Courchamp et al. 2003; Harris 2009; St Clair 2011; Harper and Bunbury 2015). Their broad diet, high fecundity and tolerance to environmental conditions have allowed them to become established in diverse environments ranging from tropical islands to polar regions (Ruffino et al. 2011), where they have contributed to declines in populations of native birds, mammals, lizards, invertebrates and plants via direct predation (Jones et al. 2008; St Clair 2011; Riofrío-Lazo and Páez-Rosas 2015).

In addition to direct predation, black rats can affect native fauna through other interspecific interactions, such as competition (Smith and Banks 2014). For example, invasive black rats are often implicated as a threat to native rodents with similar life histories (Holmes et al. 2019). However, direct evidence of competition can be challenging to quantify (Harris 2009) and is often conflated with other factors. As such, some have questioned whether the effects of black rats on native rodents may be overstated (Norman 1975; Towns et al. 2006). For example, black rats are closely associated with humans (Harper and Bunbury 2015) and, thus, native rodents' responses to black rats may actually be a function of other anthropogenic factors, such as habitat fragmentation, pollution and altered disturbance regimes, rather than competition from black rats (Harris 2009). In addition, it is often difficult to isolate the effects of a single invasive species in such contexts, as other invasive plants and animals are often present where black rats have become established (Towns et al. 2006). Given these challenges, investigating the degree of spatial or temporal overlap in habitat use or habitat characteristics, i.e. Grinnellian niche (Grinnell 1917), may provide limited insight into the degree of competition between black rats and native rodents.

In contrast to the Grinnellian conceptualisation of a species' niche, where the focus is on the environmental characteristics of a species' range, the Eltonian conceptualisation of niche focuses on functional traits and interspecific trophic interactions (Elton 1927; Sales et al. 2021), such as resource consumption (Soberón 2007). Thus, investigating the degree of overlap in Eltonian niche-space more directly corresponds to competition for resources than simply comparing spatial/ temporal overlap in environmental conditions. Furthermore, considering competition in this way allows for better understanding processes like resource limitation, foraging dynamics and survival, which directly provide information for effective conservation strategies (Manlick et al. 2021).

Though previously understudied because of lack of data (Rosado et al. 2016), investigations of Eltonian niches have expanded in recent years as stable isotopes have become a well-established tool for quantifying animal diets (Bearhop et al. 2004; Manlick et al. 2019). Specifically, the values of carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes can reveal important differences in the diets of individuals and populations (Kelly 2000), as well as variation over time and space (Ben-David et al. 1997). For example, carbon isotope ratios have been shown to correspond to the photosynthetic pathway of plants consumed (i.e. C_3, C_4 and CAM) and the proportions of marine, terrestrial and anthropogenic foods (Kelly 2000; Newsome et al. 2015). Similarly, nitrogen isotopes reflect trophic level, where δ^{15}N increases by 2–4‰ per trophic level (Crawford et al. 2008). Thus, these isotope ratios can reveal multiple ecologically meaningful aspects of animal diets.

In southern Florida, USA, diverse native wildlife communities are being transformed by multiple invasions by introduced species, making this region ideal for examining the role of competition between invasive and native species within taxonomic groups (e.g. Rodentia). Specifically, black rats have been implicated as a threat to multiple native and endangered rodents in southern Florida (Goodyear 1992; Frank et al. 1997; Boone and McCleery 2023). Empirical support for competition with black rats amongst native rodents in the region is limited to spatial and temporal overlap in occurrence and activity (McCleery et al. 2005; Taillie et al. 2020), though diet comparisons in a lab setting have suggested some differences in diet between native and invasive rats in the Florida Keys (Goodyear 1992).

We used stable isotopes to investigate the potential for competition between black rats and native rodents. Specifically, we compared the isotopic niches of invasive black rats and native rice rats (*Oryzomys* spp.) on two island groups in southern Florida, USA, which we used as a proxy for their Eltonian niches. In addition, we collected potential food items and used stable isotope mixing models to compare the diet composition amongst populations. Due to their more specialised, carnivorous diet (Sharp 1967; Goodyear 1992), we expected native rice rats to have narrower Eltonian niches (i.e. smaller ellipses in isotope space) than black rats, which are characterised by a more generalist diet. Furthermore, we expected the diets of both black rat populations to consist of mostly plants (Riofrío-Lazo and Páez-Rosas 2015; Shiels et al. 2017), compared to rice rats which specialise in consuming wetland macroinvertebrates (Sharp 1967; Goodyear 1992).

Methods

Study areas and focal species

We quantified trophic niches of four rodent populations on two island groups (hereafter: "islands") in southern Florida, USA. Each of these islands supports a small-ranging subspecies of the marsh rice rat (*O. palustris* spp.). The Sanibel island rice rat (*Oryzomys palustris sanibeli*) is endemic to the Sanibel-Captiva barrier island complex on the south-western coast of Florida (Fig. 1). It is classified as threatened in the State of Florida and is currently under review for listing as endangered/threatened under the US Endangered Species Act. Though genetically distinct from the broadly distributed marsh rice rat, Sanibel Island rice rats appear to occur in similar environments, namely freshwater herbaceous wetlands (Indorf and Gaines 2013). The silver rice rat (*Oryzomys palustris natator*) is federally endangered and endemic to the Lower Florida Keys (USFWS 2021), an island group approximately 40 km southwest of mainland Florida (Fig. 1). Unlike other subspecies of *Oryzomys palustris* spp., which tend to occur in herbaceous wetlands, silver rice rats primarily occur in tidal dwarf mangrove communities (Taillie et al. 2020). Black rats co-occur with both rice rat populations and have been implicated as a potential threat to their conservation (Taillie et al 2020; Boone and McCleery 2023). As such, we compared the isotopic signature and diet composition between silver rice rats and black rats on the Lower Keys, as well as between Sanibel island rice rats and black rats on Sanibel Island.

Sample collection and processing

On both Sanibel and the Lower Keys, we trapped areas known to support the focal subspecies of *Oryzomys palustris* spp. (i.e. Sanibel Island rice rats and silver rice rats, respectively). All rodent isotope samples were collected between 1 October and 31 December 2021. At a given site, we deployed a grid of 25 Sherman traps for four consecutive nights. Each night, traps were opened within 2 hours of sunset and closed within 3 hours of sunrise the following morning. Upon closing traps, we collected all captured rodents and recorded the species, weight, length, and sex of each. In addition, we used small scissors to collect a ~ 2 mg sample of dorsal guard hairs to be analysed for stable isotopes. Each sample was stored in a sealable plastic bag and was frozen within 12 hours. All trapping and handling methods were approved by the University of Florida Animal Use and Care Committee (#202110390).
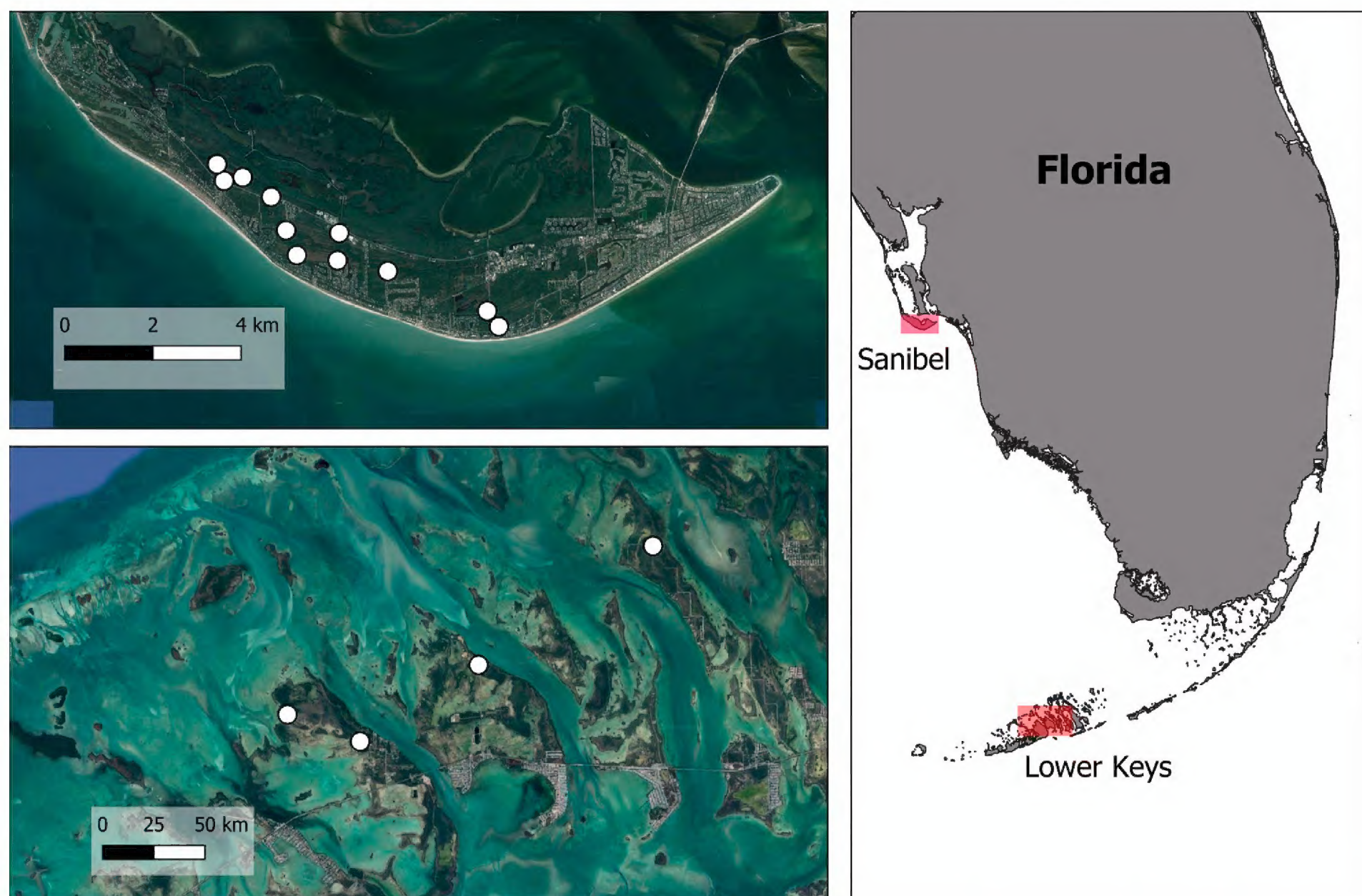
Figure 1. The location of rodent trapping locations (white circles) on each of Sanibel-Captiva Island and the Lower Florida Keys, USA (2017–2021). The right panel shows the location of these islands with respect to mainland Florida.

At each site, while traps were deployed, we opportunistically collected potential food items, based on previous studies of the diets of *Oryzomys palustris* spp. (Suppl. material 1: table S1). To represent the various potential food items of each rodent population, we aimed to collect at least two samples from each of five functional groups: plant, crustacean, fish, mollusc and other invertebrates from each island (i.e. Sanibel and Lower Keys). Based on previous literature, plant samples consisted of tissues most likely to be consumed by rodents, such as fruits, seeds and flowers (Suppl. material 1: table S1). The specific tissues collected from a specific plant were opportunistic, based on availability, but those previously documented in rodent diets were prioritised. As these samples were opportunistic, samples of the same plant species could represent different tissues. To supplement the potential food item samples collected in 2021 during the acquisition of rodent hair samples, we included 51 additional food item samples from Sanibel Island collected in a similar manner during 2017. All samples were stored in a cooler with ice upon collection and stored in a freezer within 12 hours. Prior to analysis, samples were thawed, rinsed with deionised water, dried in oven for 48 hr at 60 °C and then homogenised using a mortar and pestle. Samples were analysed at University of Florida's Light Stable Isotope Mass Spectrometry Lab for isotopic values of both carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). Two reference materials, $USGS_{40}$ (L-glutamic acid) and $USGS_{41b}$ (L-glutamic acid enriched in ^{13}C and ^{15}N) were used to calibrate the system at the beginning, end, and at regular intervals. The precision for $USGS_{40}$ was 0.07 and 0.11 for ^{13}C and ^{15}N, respectively.

Analysis

We first quantified each population's Eltonian niche by plotting the values of $\delta^{13}C$ and $\delta^{15}N$ in isotope-space. We made qualitative comparisons amongst the four populations by comparing the relative positions of individuals in isotope-space. In addition, we used an ANOVA to test for statistically significant ($p < 0.05$) differences of each isotope between rice rats and black rats on each island. We then considered the area of isotope-space occupied by a population as a metric of niche breadth. Specifically, we used the standard ellipse area corrected for small sample sizes (SEAc) to quantify and compare the isotopic niche breadth of rice rats and black rats on each island. To account for variation in sample size amongst populations and to formally account for uncertainty (Jackson et al. 2011), we used a Bayesian approach to calculate 95% prediction ellipses for each population using the R package *SIBER* v.2.6.1 (R Development Core Team 2018; Jackson and Parnell 2021). We sampled the posterior distribution over 10,000 iterations and discarded the first 1,000.

To compare the relative position of the ellipses in isotope-space, we used two metrics of ellipse overlap. First, we calculated the proportion of the overlapping area to the total area of the ellipses being compared (hereafter: "total area proportion"). This total area proportion could range from 0 (no overlap) to 1 (total overlap). As black rats are generalists (Cox et al. 2000; Ruffino et al. 2011; Shiels et al. 2013), we expected their ellipses to be larger than those of rice rats, which would influence the total area proportion. Thus, we also calculated the proportion of the area of overlap to the area of the native rodent's ellipse (hereafter "native proportion"), to serve as a complementary overlap metric that did not depend on the size of the black rat ellipse. As with the total area proportion, the native proportion could range from 0 (no overlap) to 1 (completely contained within black rat ellipse). To acknowledge uncertainty in these overlap metrics, we reported the 10th and 90th quantiles of the posterior sample of each metric.

To link isotope signatures from rodent tissues to food items and make inferences about rodent diets, we used stable isotope mixing models using the R package *simmr* (Parnell 2021). We first grouped the food items according to three broad taxa: animals, C_3 plants and C_4 plants. We based these categories not only on consumer diet (e.g. herbivore, omnivore), but also on clustering of isotope values within groups. For example, C_4 plants were enriched in $\delta^{13}C$ and isotopically distinct relative to C_3 plants and the strong differentiation in $\delta^{13}C$ we observed corresponded closely to the reported ranges for plants using C_3 photosynthesis (range = –35 to –21‰) and C_4 photosynthesis (range = –14 to –10‰; (Kelly 2000)). To accommodate variable rates of isotope discrimination during assimilation and excretion (Olive et al. 2003), we adjusted isotope values using diet-tissue discrimination factors (TDF; Phillips et al. 2014). In addition to the consumer tissue being analysed, the consumer's diet can also influence the TDF (Stephens et al. 2022). Thus, we used previously reported TDF's for hair samples from omnivorous mammals (1.5 and 2.8 for $\delta^{13}C$ and $\delta^{15}N$, respectively; (Stephens et al. 2022)), which were consistent with those used previously in southern Florida (Cove et al. 2018). We fitted the mixing models using the simmr_mcmc function with 100,000 iterations of four chains thinned by every 10th iteration and a burn-in of 10,000 iterations. We checked for model convergence by ensuring the Rhat statistic was less than 1.05 for all estimated parameters (Parnell 2021). We used the compare_groups function to determine the probability that the diet proportion for a given food was different between two populations. We considered probabilities greater than 0.9 to have strong support.

Results

Our rodent trapping efforts resulted in hair samples from 23 silver rice rats and 18 black rats on the Lower Keys, as well as 9 Sanibel Island rice rats and 17 black rats on Sanibel. Though we trapped 11 sites on Sanibel Island where Sanibel Island rice rats were captured previously, we only detected them at three of these 11 sites. Meanwhile, we collected 78 potential food items, which we supplemented with 51 additional items collected from Sanibel in 2017 (Suppl. material 1: table S2). Isotope values for all rodent hair samples (including 30 Sanibel Island rice rat samples not included in this analysis) and food item samples are provided in the supplemental material (Suppl. material 1: table S3).

Broadly, we observed greater values of both $\delta^{13}C$ and $\delta^{15}N$ in rice rats compared to black rats on their respective islands (Table 1). The means of both isotopes were significantly (ANOVA $p < 0.05$) greater for rice rats compared to black rats on both islands. When considering both isotopes simultaneously, the standard ellipse areas were smaller for rice rats compared to their respective populations of black rats, but the 95% credible intervals overlapped for these comparisons. The ellipses for all four populations of rodents overlapped in isotope-space (Fig. 2). The 95% credible intervals for the total area proportion were 0.05–0.35 and 0.17–0.38, on Sanibel and the Lower Keys, respectively. The native area proportion was more variable, with the 95% credible intervals ranging from 0.09–0.59 and 0.27–0.72, respectively.
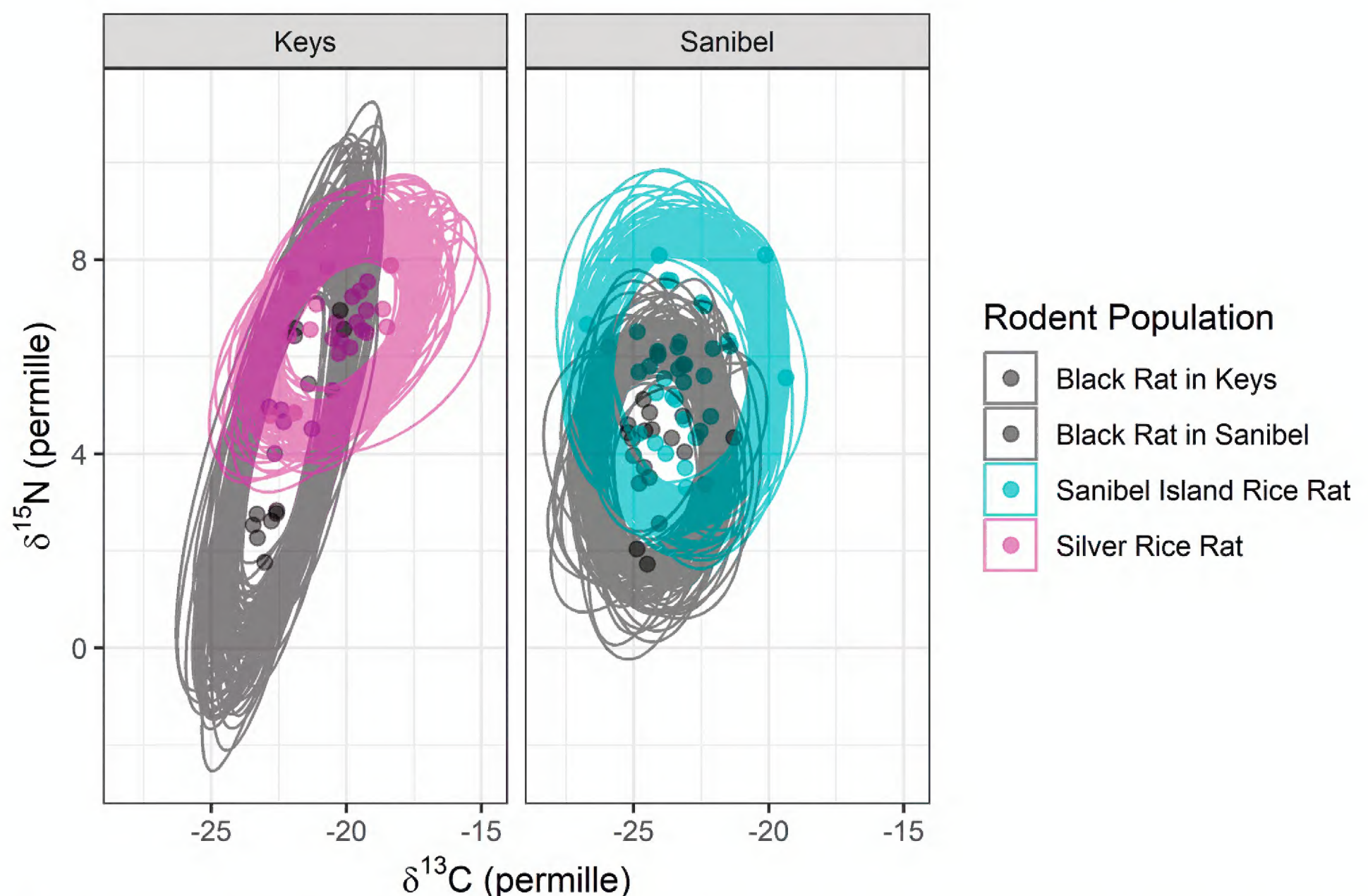

Figure 2. The nitrogen and carbon stable isotope values for four populations of rodents on two islands (Lower Keys and Sanibel-Captiva) in southern Florida, USA. The corresponding ellipses represent the posterior distributions of estimated bi-variate ellipses used to compare isotopic overlap. Shown also are the means (black dots) and standard deviations (coloured crosses) of the stable isotope values of the three taxa of potential food items (i.e. sources).

Table 1. Minimum and maximum isotopic values and Standard Ellipse Area with small sample correction for four populations of rodents in southern Florida, USA.

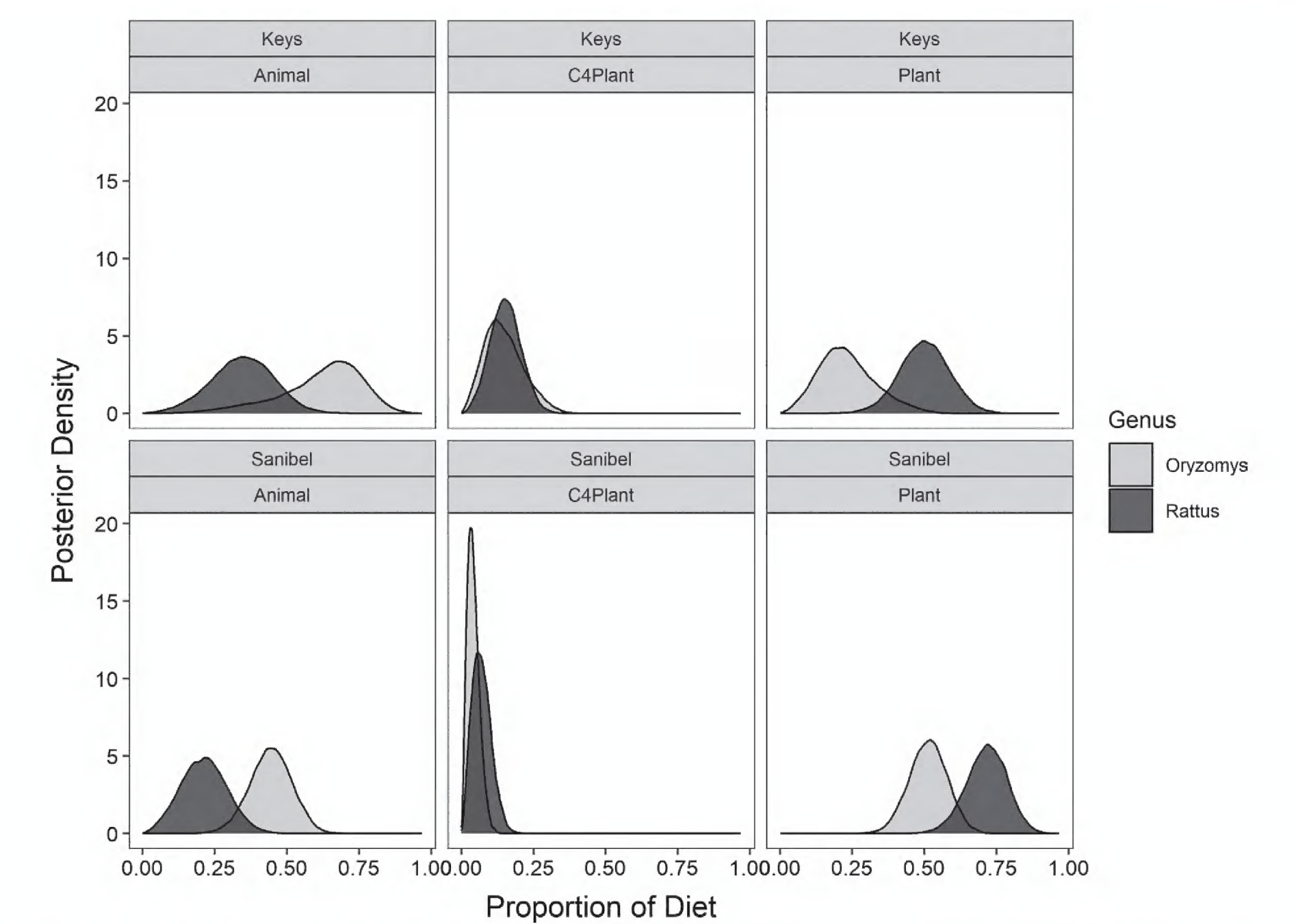| Species	Island	Range δ¹³C	Range δ¹⁵N	Mean δ¹³C	Mean δ¹⁵N	SEAc
Silver Rice Rat	Keys	-22.8, -18.4	4.8, 7.9	-20.2	6.6	2.9
Black Rat	Keys	-23.5, -20.1	1.8, 7.0	-22.2	4.3	3.4
Sanibel Island Rice Rat	Sanibel	-23.6, -20.1	5.5, 8.1	-22.7	6.6	2.7
Black Rat	Sanibel	-25.2, -21.3	1.7, 5.1	-24.3	3.9	3.1

Figure 3. Posterior distributions and boxplots comparing the relative proportion of three food categories (animal, C3 plant and C4 plant) between two genera of rodents (rice rats [*Oryzomys*] and black rats [*Rattus*]) in each of two islands in southern Florida, USA (the Lower Keys and Sanibel-Captiva; 2021). Included in each panel is the probability (P) that the food item's proportional composition of diet is greater for one genus when compared to the other.

Despite this overlap, stable isotope mixing models suggested the diets of native rice rats differed from those of black rats on their respective islands. On the Keys, there was a high probability (P > 0.9) that rice rats consumed more animals and fewer plants compared to black rats, which consumed more plants (Fig. 3). We observed similar differences on Sanibel; however, the low sample size of Sanibel Island rice rats resulted in greater uncertainty in diet proportions. On the Lower Keys, the 95% credible intervals of the diet proportions were wider and, thus, the differences were less significant (Suppl. material 1: fig. S1). However, both these data, as well as unpublished data from Sanibel Island rice rat samples collected in 2017 (Suppl. material 1: table S3) reflect a similar diet of approximately equal parts plant and animal, compared to black rats which ate mostly plants (Fig. 3).

When we compared between islands, we observed strong evidence that the diet of black rats on Sanibel consisted of more plants than black rats on the Keys. Otherwise, comparisons within species between islands did not exceed the 0.9 probability threshold.

Discussion

Consistent with our expectation, the isotopic niche of black rats was larger than that of rice rats, reflecting a more generalist diet. Both rice rat populations appeared to be more carnivorous than black rats, evidenced by greater $\delta^{15}N$ than black rats on their respective islands. However, there was considerable overlap in isotope-space between rice rats and black rats on both islands. Despite this overlap, we observed two important differences in diet. First, rice rats consumed comparable amounts of animal and plant foods, compared to both populations of black rats, which ate mostly plants. On the Keys specifically, rice rats consumed mostly animal foods. These differences in diet suggest competition between native rice rats and exotic black rats may be limited. Second, the diet composition and stable isotope signatures of closely related rodents, as well as the food they consume, differed between the islands we investigated suggesting that the relative impact of black rats on native rodents may vary considerably.

Broadly, we observed that rice rats specialised in animal foods, whereas black rats consumed mostly plants, which is consistent with other studies of rodent diets (Goodyear 1992; Shiels et al. 2013; Riofrío-Lazo and Páez-Rosas 2015). Specifically, for silver rice rats on the Lower Keys, these differences in diet are further supported by temporal niche partitioning between silver rice rats and black rats, where the former are most active at low tide when tidal macroinvertebrates are more available (Taillie et al. 2020). Given that black rats have co-occurred with native rodents on Caribbean islands for several centuries (Harper and Bunbury 2015), some degree of partitioning is requisite for the continued co-existence of native and invasive rodents (Hardin 1960; MacArthur and Levins 1967).

Importantly, we observed some notable differences between the Lower Keys and Sanibel. Though rice rats on both island groups consumed primarily animal foods, plants represented a larger proportion of rice rat diets on Sanibel. Similarly, black rats on Sanibel consumed proportionally more plants compared to black rats on the Lower Keys. These between-island differences could result from differences in marine subsidies that have been shown to be important to mammalian diets (Stapp and Polis 2003; Manlick et al. 2019; Davidson et al. 2021). Specifically, silver rice rats in the Lower Keys may rely more on tidal macroinvertebrates compared to Sanibel where water levels are less variable and the vegetation community is less salt-tolerant (Indorf and Gaines 2013). More generally, previous research has suggested that Eltonian niches are driven by environmental factors such as landscape composition and prey availability (Manlick et al. 2019) and even species considered to be specialists can exhibit Eltonian niche plasticity (Terry et al. 2017). As such, the degree of competition between native rodents and invasive black rats likely varies as a function of environmental context and geography. Other studies have suggested that competition from black rats may limit populations of rodents on other islands (Harris and Macdonald 2007; Harper and Cabrera 2010; Russell et al. 2015), which could result from differences in resource availability, as well as traits of competing species.

On both islands, isotope signatures of rice rats and black rats differed more in the values of $\delta^{15}N$ than $\delta^{13}C$, suggesting that these differences in diets were driven more by trophic levels than primary producer photosynthetic pathways. The minimal differentiation in $\delta^{13}C$ was surprising given that we expected differential consumption of native C4 plants (e.g. grasses), C4 plants in anthropogenic foods (e.g. corn) and marine foods between rodent populations, all of which have been shown previously to influence $\delta^{13}C$ (Ben-David et al. 1997; Kelly 2000; Newsome et al. 2015). For example, previous work has suggested that anthropogenic food subsidies likely drove $\delta^{13}C$ enrichment in feral cats (*Felis catus*) on the Florida Keys (Cove et al. 2018). However, the individuals in our study may consume fewer anthropogenic foods, given the wetland environments away from human development in which our study took place.

One important limitation of our study is that we only sampled rodent diets during a single season (late autumn/early winter). Previous studies have shown that stable isotopes can vary seasonally as a function of diet, as well as other factors (Ben-David et al. 1997; Willson et al. 2010). Though temperature variation in the subtropical climate of southern Florida are minimal, seasonal variation in precipitation has been shown to be an important driver of animal phenology and demographics (Henry et al. 2022). As such, resource abundance and, as a result, diet and competition of rice rats and black rats are likely to change seasonally. Future work should focus specifically on times of the year when resources are limited to better understand how those limited resources are partitioned between sympatric species.

Our results suggest that the degree of competition between black rats and native rodents may vary as a function of environmental factors, such as prey availability and geographical context. Consequently, responses amongst native rodents to invasive black rats and the need for control or eradication efforts may also vary. Therefore, previously documented conservation successes for taxa such as seabirds resulting from invasive rat eradication efforts (Jones et al. 2016) may not translate to similar benefits for the conservation of native rodents. In addition, eradication of invasive rats is expensive and can have unintended negative consequences for both native rodents and other taxa (Simberloff 2001; Howald et al. 2010). In contexts where competition from invasive rats is limited, conservation practitioners should work to identify and address more direct threats limiting the populations of threatened species, such as habitat loss and other anthropogenic stressors.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: RM, WWBI, PT. Data curation: WWBI, ALWS, PT. Formal analysis: PT. Funding acquisition: PT, RM. Investigation: ALWS. Methodology: ALWS, RM, WWBI. Project administration: RM, PT. Supervision: WWBI. Writing – original draft: PT. Writing – review and editing: RM.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Data and summary statistics

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